

AD-A156 774

AQUATIC PLANT CONTROL RESEARCH PROGRAM A MATHEMATICAL
MODEL OF SUBMERSED... (U) RENSSELAER POLYTECHNIC INST
TROY NY CENTER FOR ECOLOGICAL MOD... C D COLLINS ET AL.
MAY 85 WES/MP/A-85-2 DACW39-81-C-0036

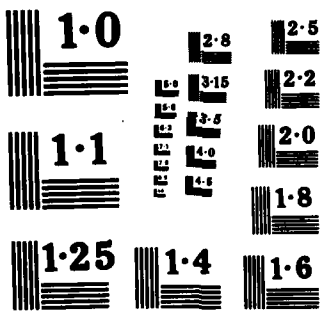
1/8

UNCLASSIFIED

F/G 8/8

NL

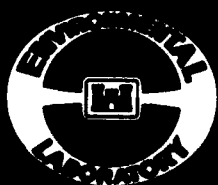
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295
296
297
298
299
300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355
356
357
358
359
360
361
362
363
364
365
366
367
368
369
370
371
372
373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394
395
396
397
398
399
400
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432
433
434
435
436
437
438
439
440
441
442
443
444
445
446
447
448
449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
483
484
485
486
487
488
489
490
491
492
493
494
495
496
497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558
559
560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631
632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651
652
653
654
655
656
657
658
659
660
661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698
699
700
701
702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733
734
735
736
737
738
739
740
741
742
743
744
745
746
747
748
749
750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808
809
810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826
827
828
829
830
831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863
864
865
866
867
868
869
870
871
872
873
874
875
876
877
878
879
880
881
882
883
884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946
947
948
949
950
951
952
953
954
955
956
957
958
959
960
961
962
963
964
965
966
967
968
969
970
971
972
973
974
975
976
977
978
979
980
981
982
983
984
985
986
987
988
989
990
991
992
993
994
995
996
997
998
999
1000
1001
1002
1003
1004
1005
1006
1007
1008
1009
1010
1011
1012
1013
1014
1015
1016
1017
1018
1019
1020
1021
1022
1023
1024
1025
1026
1027
1028
1029
1030
1031
1032
1033
1034
1035
1036
1037
1038
1039
1040
1041
1042
1043
1044
1045
1046
1047
1048
1049
1050
1051
1052
1053
1054
1055
1056
1057
1058
1059
1060
1061
1062
1063
1064
1065
1066
1067
1068
1069
1070
1071
1072
1073
1074
1075
1076
1077
1078
1079
1080
1081
1082
1083
1084
1085
1086
1087
1088
1089
1090
1091
1092
1093
1094
1095
1096
1097
1098
1099
1100
1101
1102
1103
1104
1105
1106
1107
1108
1109
1110
1111
1112
1113
1114
1115
1116
1117
1118
1119
1120
1121
1122
1123
1124
1125
1126
1127
1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160
1161
1162
1163
1164
1165
1166
1167
1168
1169
1170
1171
1172
1173
1174
1175
1176
1177
1178
1179
1180
1181
1182
1183
1184
1185
1186
1187
1188
1189
1190
1191
1192
1193
1194
1195
1196
1197
1198
1199
1200
1201
1202
1203
1204
1205
1206
1207
1208
1209
1210
1211
1212
1213
1214
1215
1216
1217
1218
1219
1220
1221
1222
1223
1224
1225
1226
1227
1228
1229
1230
1231
1232
1233
1234
1235
1236
1237
1238
1239
1240
1241
1242
1243
1244
1245
1246
1247
1248
1249
1250
1251
1252
1253
1254
1255
1256
1257
1258
1259
1260
1261
1262
1263
1264
1265
1266
1267
1268
1269
1270
1271
1272
1273
1274
1275
1276
1277
1278
1279
1280
1281
1282
1283
1284
1285
1286
1287
1288
1289
1290
1291
1292
1293
1294
1295
1296
1297
1298
1299
1300
1301
1302
1303
1304
1305
1306
1307
1308
1309
1310
1311
1312
1313
1314
1315
1316
1317
1318
1319
1320
1321
1322
1323
1324
1325
1326
1327
1328
1329
1330
1331
1332
1333
1334
1335
1336
1337
1338
1339
1340
1341
1342
1343
1344
1345
1346
1347
1348
1349
1350
1351
1352
1353
1354
1355
1356
1357
1358
1359
1360
1361
1362
1363
1364
1365
1366
1367
1368
1369
1370
1371
1372
1373
1374
1375
1376
1377
1378
1379
1380
1381
1382
1383
1384
1385
1386
1387
1388
1389
1390
1391
1392
1393
1394
1395
1396
1397
1398
1399
1400
1401
1402
1403
1404
1405
1406
1407
1408
1409
1410
1411
1412
1413
1414
1415
1416
1417
1418
1419
1420
1421
1422
1423
1424
1425
1426
1427
1428
1429
1430
1431
1432
1433
1434
1435
1436
1437
1438
1439
1440
1441
1442
1443
1444
1445
1446
1447
1448
1449
1450
1451
1452
1453
1454
1455
1456
1457
1458
1459
1460
1461
1462
1463
1464
1465
1466
1467
1468
1469
1470
1471
1472
1473
1474
1475
1476
1477
1478
1479
1480
1481
1482
1483
1484
1485
1486
1487
1488
1489
1490
1491
1492
1493
1494
1495
1496
1497
1498
1499
1500
1501
1502
1503
1504
1505
1506
1507
1508
1509
1510
1511
1512
1513
1514
1515
1516
1517
1518
1519
1520
1521
1522
1523
1524
1525
1526
1527
1528
1529
1530
1531
1532
1533
1534
1535
1536
1537
1538
1539
1540
1541
1542
1543
1544
1545
1546
1547
1548
1549
1550
1551
1552
1553
1554
1555
1556
1557
1558
1559
1560
1561
1562
1563
1564
1565
1566
1567
1568
1569
1570
1571
1572
1573
1574
1575
1576
1577
1578
1579
1580
1581
1582
1583
1584
1585
1586
1587
1588
1589
1590
1591
1592
1593
1594
1595
1596
1597
1598
1599
1600
1601
1602
1603
1604
1605
1606
1607
1608
1609
1610
1611
1612
1613
1614
1615
1616
1617
1618
1619
1620
1621
1622
1623
1624
1625
1626
1627
1628
1629
1630
1631
1632
1633
1634
1635
1636
1637
1638
1639
1640
1641
1642
1643
1644
1645
1646
1647
1648
1649
1650
1651
1652
1653
1654
1655
1656
1657
1658
1659
1660
1661
1662
1663
1664
1665
1666
1667
1668
1669
1670
1671
1672
1673
1674
1675
1676
1677
1678
1679
1680
1681
1682
1683
1684
1685
1686
1687
1688
1689
1690
1691
1692
1693
1694
1695
1696
1697
1698
1699
1700
1701
1702
1703
1704
1705
1706
1707
1708
1709
1710
1711
1712
1713
1714
1715
1716
1717
1718
1719
1720
1721
1722
1723
1724
1725
1726
1727
1728
1729
1730
1731
1732
1733
1734
1735
1736
1737
1738
1739
1740
1741
1742
1743
1744
1745
1746
1747
1748
1749
1750
1751
1752
1753
1754
1755
1756
1757
1758
1759
1760
1761
1762
1763
1764
1765
1766
1767
1768
1769
1770
1771
1772
1773
1774
1775
1776
1777
1778
1779
1780
1781
1782
1783
1784
1785
1786
1787
1788
1789
1790
1791
1792
1793
1794
1795
1796
1797
1798
1799
1800
1801
1802
1803
1804
1805
1806
1807
1808
1809
1810
1811
1812
1813
1814
1815
1816
1817
1818
1819
1820
1821
1822
1823
1824
1825
1826
1827
1828
1829
1830
1831
1832
1833
1834
1835
1836
1837
1838
1839
1840
1841
1842
1843
1844
1845
1846
1847
1848
1849
1850
1851
1852
1853
1854
1855
1856
1857
1858
1859
1860
1861
1862
1863
1864
1865
1866
1867
1868
1869
1870
1871
1872
1873
1874
1875
1876
1877
1878
1879
1880
1881
1882
1883
1884
1885
1886
1887
1888
1889
1890
1891
1892
1893
1894
1895
1896
1897
1898
1899
1900
1901
1902
1903
1904
1905
1906
1907
1908
1909
1910
1911
1912
1913
1914
1915
1916
1917
1918
1919
1920
1921
1922
1923
1924
1925
1926
1927
1928
1929
1930
1931
1932
1933
1934
1935
1936
1937
1938
1939
1940
1941
1942
1943
1944
1945
1946
1947
1948
1949
1950
1951
1952
1953
1954
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
2022
2023
2024
2025
2026
2027
2028
2029
2030
2031
2032
2033
2034
2035
2036
2037
2038
2039
2040
2041
2042
2043
2044
2045
2046
2047
2048
2049
2050
2051
2052
2053
2054
2055
2056
2057
2058
2059
2060
2061
2062
2063
2064
2065
2066
2067
2068
2069
2070
2071
2072
2073
2074
2075
2076
2077
2078
2079
2080
2081
2082
2083
2084
2085
2086
2087
2088
2089
2090
2091
2092
2093
2094
2095
2096
2097
2098
2099
2100
2101
2102
2103
2104
2105
2106
2107
2108
2109
2110
2111
2112
2113
2114
2115
2116
2117
2118
2119
2120
2121
2122
2123
2124
2125
2126
2127
2128
2129
2130
2131
2132
2133
2134
2135
2136
2137
2138
2139
2140
2141
2142
2143
2144
2145
2146
2147
2148
2149
2150
2151
2152
2153
2154
2155
2156
2157
2158
2159
2160
2161
2162
2163
2164
2165
2166
2167
2168
2169
2170
2171
2172
2173
2174
2175
2176
2177
2178
2179
2180
2181
2182
2183
2184
2185
2186
2187
2188
2189
2190
2191
2192
2193
2194





US Army Corps
of Engineers

AD-A156 774



**AQUATIC PLANT CONTROL
RESEARCH PROGRAM**

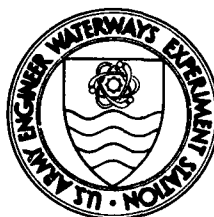
MISCELLANEOUS PAPER A-85-2

**A MATHEMATICAL MODEL OF
SUBMERSED AQUATIC PLANTS**

by

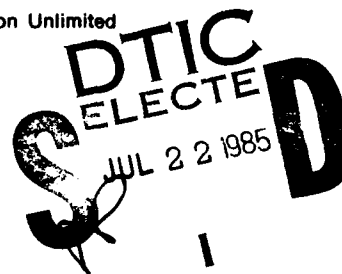
Carol Desormeau Collins, Richard A. Park, Charles W. Boylen

Center for Ecological Modeling
Rensselaer Polytechnic Institute
Troy, New York 12181



May 1985
Final Report

Approved For Public Release; Distribution Unlimited



DTIC FILE COPY

Prepared for DEPARTMENT OF THE ARMY
US Army Corps of Engineers
Washington, DC 20314-1000

Under Contract No. DACW39-81-C-0036

Monitored by Environmental Laboratory
US Army Engineer Waterways Experiment Station
PO Box 631, Vicksburg, Mississippi 39180-0631

85 07 09 02 5

Destroy this report when no longer needed. Do not return
it to the originator.

The findings in this report are not to be construed as an official
Department of the Army position unless so designated
by other authorized documents.

The contents of this report are not to be used for
advertising, publication, or promotional purposes.
Citation of trade names does not constitute an
official endorsement or approval of the use of
such commercial products.

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER Miscellaneous Paper A-85-2	2. GOVT ACCESSION NO. AD-A156 074	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) A MATHEMATICAL MODEL OF SUBMERSED AQUATIC PLANTS	5. TYPE OF REPORT & PERIOD COVERED Final report	
7. AUTHOR(s) Carol Desormeau Collins, Richard A. Park, Charles W. Boylen	6. PERFORMING ORG. REPORT NUMBER	
9. PERFORMING ORGANIZATION NAME AND ADDRESS Rensselaer Polytechnic Institute Center for Ecological Modeling Troy, New York 12181	8. CONTRACT OR GRANT NUMBER(s) Contract No. DACW39-81-C-0036	
11. CONTROLLING OFFICE NAME AND ADDRESS DEPARTMENT OF THE ARMY US Army Corps of Engineers Washington, DC 20314-1000	10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS Aquatic Plant Control Research Program	
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) US Army Engineer Waterways Experiment Station Environmental Laboratory PO Box 631, Vicksburg, Mississippi 39180-0631	12. REPORT DATE May 1985	
	13. NUMBER OF PAGES 37	
	15. SECURITY CLASS. (of this report) Unclassified	
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES Available from National Technical Information Service, 5285 Port Royal Road, Springfield, Virginia 22161.		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Aquatic ecology (LC) Aquatic plants--Mathematical models; (LC) GE-QUAL-R1 (WES) Eurasian watermilfoil; (LC) and Hydrilla (LC) Water quality management, (LC)		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Submersed aquatic plants or macrophytes often contribute significantly to primary production in lakes and reservoirs. Macrophyte growth and decomposi- tion can influence the physical, chemical, and biological characteristics of aquatic ecosystems, including temperature and concentrations of dissolved oxy- gen, nitrogen, phosphorus, inorganic carbon, detritus, phytoplankton, and fish.		

(Continued)

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE(When Data Entered)

20. ABSTRACT (Continued).

A mathematical model of submersed aquatic macrophyte growth and decomposition was developed for use with the US Army Corps of Engineers' one-dimensional reservoir water quality model, CE-QUAL-R1, which was developed under the Environmental and Water Quality Operational Studies (EWQOS). The ecological processes recommended for inclusion with the macrophyte compartment include gross production, dark respiration, photorespiration, nonpredatory mortality, and grazing. The influence of these processes on other compartments in CE-QUAL-R1 is described.

Select process equations have been validated using a stand-alone version of the recommended model based upon experimental results derived from the literature and other research at the US Army Engineer Waterways Experiment Station for two macrophyte species, *Myriophyllum spicatum* and *Hydrilla verticillata*. Management control strategies can be simulated for mechanical harvesting and chemical control of the plants. *Remarks:*

Accession For	
NTIS GRA&I	<input checked="checked" type="checkbox"/>
DTIC TAB	<input type="checkbox"/>
Unannounced	<input type="checkbox"/>
Justification	
Pr	
Distribution/	
Availability Codes	
Dist	Avail and/or Special
A-1	

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE(When Data Entered)

Preface

This investigation was supported by the Aquatic Plant Control Research Program (APCRP), sponsored by the Office, Chief of Engineers (OCE), and was managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. The OCE Technical Monitor was Mr. E. Carl Brown.

This is the final report for Contract No. DACW39-81-C-0036, "A Mathematical Model of Submersed Aquatic Plants," prepared by Rensselaer Polytechnic Institute (RPI), Troy, N. Y. Authors of this report were Drs. Carol Desormeau Collins, Richard A. Park, and Charles W. Boylen, RPI. The model was conceptualized and developed for incorporation into the US Army Corps of Engineers' reservoir water quality model, CE-QUAL-R1, which was developed during the conduct of the Environmental and Water Quality Operational Studies (EWQOS). CE-QUAL-R1 is a numerical, one-dimensional model that describes the vertical distribution of thermal energy and biological and chemical materials in a reservoir through time. The mathematical structure of the model is based on horizontal layers; temperature and materials concentration gradients are computed only in the vertical direction.

The original contract called for the development of algorithms and the programming of those algorithms for inclusion in CE-QUAL-R1. However, in subsequent discussions with the contract officer at the time, Mr. Joseph Norton, Environmental Research and Simulation Division (ERSD), and with other staff of the WES, Environmental Laboratory (EL), including Drs. Joseph H. Wlosinski and Allan S. Lessem, it was agreed that the programming should be done by the Environmental Laboratory staff most familiar with CE-QUAL-R1. The draft report was reviewed by Drs. Wlosinski and Lessem and Messrs. Mark S. Dortch and Jack B. Waide.

Manager of the APCRP was Mr. J. Lewis Decell. General supervision was provided by Mr. Donald L. Robey, Chief, ERSD. Chief of the EL during the conduct of this investigation was Dr. John Harrison.

Commanders and Directors of WES during the study and preparation of the report were COL Tilford C. Creel, CE, and COL Robert C. Lee, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

Collins, C. D., Park, R. A., and Boylen, C. W. 1985. "A Mathematical Model of Submersed Aquatic Plants," Miscellaneous Paper A-85-2, prepared by Rensselaer Polytechnic Institute, Troy, N. Y., for the US Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Contents

	<u>Page</u>
Preface	1
Introduction	4
Background	4
Report composition	6
Recommended Physiologic Processes	6
Macrophyte processes	7
Interactions with other compartments in CE-QUAL-R1	11
Spatial Relationships	12
Management Control Processes	15
Process Validation	16
Recommendations	19
References	19
Appendix A: Macrophyte Model Stand-Alone Version	A1
Introduction	A1
State Variable Equations	A2
Process Equations	A3
Appendix B: Macrophyte Model Parameter List	B1

A MATHEMATICAL MODEL OF SUBMERSED AQUATIC PLANTS

7

Introduction

Background

1. Submersed aquatic plants or macrophytes often contribute significantly to the productivity of lakes and reservoirs. Macrophytes can become so abundant that they become a nuisance to recreational and navigational activities. Their growth and decomposition also influence other biotic and abiotic components of the ecosystem. The littoral community of many eutrophic systems is often dominated by a single species of macrophyte. Under less eutrophic conditions, several species may coexist. The growth of aquatic plants is controlled by many factors, including (a) growth properties of the plant; (b) physical factors such as temperature, irradiance levels, and changes in water elevation; and (c) physiological characteristics of the plant such as nutrient requirements, photoadaptation, and sediment preference.

2. The importance of macrophytes to the aquatic ecosystem necessitated the development and incorporation of a macrophyte submodel in the US Army Corps of Engineers' one-dimensional reservoir water quality model, CE-QUAL-R1 (Environmental Laboratory 1982), which was developed during the conduct of the Environmental and Water Quality Operational Studies (EWQOS). This report describes the development and formulation of this macrophyte submodel for inclusion in CE-QUAL-R1. The model simulates growth and decomposition of macrophytes. The influence of the plants on other compartments in CE-QUAL-R1 is also included in the model.

3. To make the proposed submodel complementary with CE-QUAL-R1, the following recommendations are made regarding the computation and layering scheme of CE-QUAL-R1. Macrophytes should be regarded as occupying the bottom surface of each layer in the reservoir within the euphotic zone. As such, they are not subject to advection or diffusion and are not transported in inflowing or outflowing waters. The macrophyte compartment should have units of grams per layer. As the layers are resized in CE-QUAL-R1, dependent on the balance of inflowing and outflowing waters, the macrophyte biomass should be reapportioned to reflect the appropriate densities for those layers. If the surface elevation drops, macrophytes in the dewatered zone should no longer be included in the computation. If the water surface elevation increases and

inundates new areas, the macrophyte density in the new area should be given a small "seed" value to represent colonization.

4. Irradiance reaching a particular model layer determines the plants' growth response. Changes in water level can affect irradiance at a particular level. Drawdown may suddenly expose submersed plants to higher irradiances as the depth of water through which light is transmitted decreases. Conversely, an increase in reservoir pool elevation may result in greater light attenuation. Light attenuation for a particular layer in CE-QUAL-R1 is dependent upon the extinction coefficient of water and on shading by suspended solids, detritus, zooplankton, and phytoplankton. It is recommended that self-shading for macrophytes also be included in the model.

5. The following processes are recommended for inclusion in the macrophyte model: gross production, dark respiration, photorespiration, nonpredatory mortality, and grazing. Control measures affecting macrophytes, such as mechanical harvesting and herbicidal treatment, should also be included in the model as described in this report. Decomposition processes already modeled in CE-QUAL-R1 would be affected by macrophyte contributions to existing detritus and sediment compartments. A flow diagram of the interactions of the new macrophyte compartment with other model compartments summarizes the proposed changes to CE-QUAL-R1 (Figure 1).

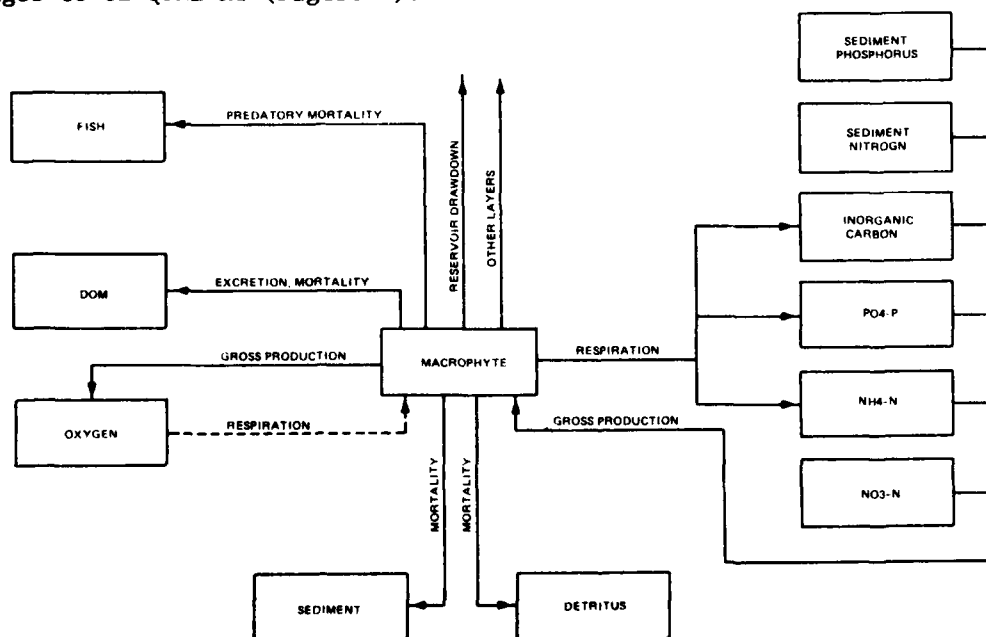


Figure 1. Compartment diagram of macrophyte model recommended for CE-QUAL-R1

Report composition

6. In the following section the specific physiological processes recommended for inclusion in a new macrophyte subroutine are formulated for incorporation into CE-QUAL-R1. Next, a geometric scheme for apportioning macrophyte biomass among model layers is discussed. The next major section contains recommendations for the simulation of macrophyte control measures (mechanical harvesting, herbicidal treatment). The next section discusses the validation of select process formulations based upon published data on two macrophyte species, *Myriophyllum spicatum* and *Hydrilla verticillata*. The final section summarizes the major recommendations contained in this report. Two appendices are also included. Appendix A presents equations included in a stand-alone version of the macrophyte submodel used in the process validation studies, while Appendix B lists representative values for parameters included in the proposed macrophyte submodel based on published research on *M. spicatum* and *H. verticillata*. The material contained in this report will be included in a final, revised edition of the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) scheduled for publication in 1985.

Recommended Physiologic Processes

7. The differential equation for the macrophyte state variable expresses conservation of mass in each horizontal model layer. The solution provides material concentrations as functions of time and depth. The equation is mathematically expressed as follows:

$$\left[\begin{array}{l} \text{rate of} \\ \text{change} \\ \text{of mass} \\ \text{g day}^{-1} \end{array} \right] = \left[\begin{array}{l} \text{macrophyte} \\ \text{biomass} \end{array} * \begin{array}{l} \text{gross} \\ \text{production} \\ \text{rate} \end{array} - \begin{array}{l} \text{dark} \\ \text{respiration} \\ \text{rate} \end{array} - \begin{array}{l} \text{photorespiration} \\ \text{rate} \end{array} \right. \\ \left. - \begin{array}{l} \text{grazing} \\ \text{rate} \end{array} - \begin{array}{l} \text{nonpredatory} \\ \text{mortality} \\ \text{rate} \end{array} - \begin{array}{l} \text{mechanical} \\ \text{or} \\ \text{chemical} \\ \text{harvesting} \\ \text{rate} \end{array} \right] \quad (1)$$

Each of the individual terms in this equation is discussed in the subsections which follow. The style of presentation follows that contained in the

CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) which should be consulted for further details. The overall structure of CE-QUAL-R1 will not be presented here. Only those macrophyte process terms specifically included in the proposed new macrophyte submodel will be documented plus their interactions with other compartments in CE-QUAL-R1.

Macrophyte processes

8. Gross production. The daily photosynthetic or gross production rate is a function of temperature, light intensity, and nutrient concentration:

$$PLTGRO = PLTMAX * RMULT1(T) * RMULT2(T) * MIN(XLIMN, XLIMP, XLIMC) * XLIML \quad (2)$$

where

PLTGRO = photosynthetic rate, day⁻¹

PLTMAX = user-specified maximum photosynthetic rate, day⁻¹

RMULT1,2(T) = temperature limitation functions, unitless

XLIMN = limitation function for nitrogen, unitless

XLIMP = limitation function for phosphorus, unitless

XLIMC = limitation function for carbon, unitless

XLIML = limitation function for light intensity, unitless

9. Temperature limitation is calculated using the equations developed by Thornton and Lessem (1978):

$$\begin{aligned}
 RMULT1(T) &= \begin{cases} 0 & T \leq T_1 \\ \frac{K_1 e^{\lambda_1 (T - T_1)}}{1 + K_1 e^{\lambda_1 (T - T_1)} - 1} & T > T_1 \end{cases} \\
 RMULT2(T) &= \begin{cases} \frac{K_4 e^{\lambda_2 (T_4 - T)}}{1 + K_4 e^{\lambda_2 (T_4 - T)} - 1} & T < T_4 \\ 0 & T \geq T_4 \end{cases}
 \end{aligned} \quad (3)$$

where

$$\lambda_1 = \frac{1}{T_2 - T_1} \ln \frac{K_2(1 - K_1)}{K_1(1 - K_2)}$$

$$\lambda_2 = \frac{1}{T_4 - T_3} \ln \frac{K_3(1 - K_4)}{K_4(1 - K_3)}$$

As is the case in the parent model CE-QUAL-R1, T_1 and T_4 represent the user-specified lower and upper lethal temperatures for the processes in question, while T_2 and T_3 (also user specified) define the range of optimum temperatures over which the process occurs at near the maximum rate (Environmental Laboratory 1982). The term T represents the computed temperature of a specific layer in the model CE-QUAL-R1. The corresponding user-specified K values define the relative rates (i.e., on a 0 to 1 basis) at which the process occurs at each of these temperatures.

10. Nutrient limitation is dependent upon the concentrations of nitrogen and phosphorus in the water column and sediment and on the carbon concentration in the water column. The nutrient determined to be limiting based upon the following Monod equation is used in the photosynthesis calculation (Equation 2):

$$XLIM(N,C,P) = \frac{C}{K_{1/2} + C} \quad (4)$$

where

$XLIM(N,C,P)$ = nutrient limitation function for nitrogen, carbon, and phosphorus, unitless

C = concentration of respective nutrient in the water column (N , C , P) or sediment (N , P), $g\ m^{-3}$

$K_{1/2}$ = user-specified half-saturation coefficient for the respective nutrient, $g\ m^{-3}$

The limiting nutrient is defined in this context as the one giving the minimum value of Equation 4.

11. Many nutrients used by freshwater submersed macrophytes, including both nitrogen and phosphorus, are obtained primarily through the roots from sediment (Best and Mantai 1978; Bole and Allan 1978; Carignan and Kalff 1980; DeMarte and Hartman 1974; Nichols and Kinney 1976). CE-QUAL-R1 has

APPENDIX A: MACROPHYTE MODEL STAND-ALONE VERSION

Introduction

1. A stand-alone version of the macrophyte model was developed to verify and validate several of the recommended process equations for a single model layer. This appendix provides a list of the state variable equations used in this version of the model. Seven compartments are represented by the model, including macrophytes, dissolved oxygen, particulate organic matter (POM), dissolved organic matter (DOM), phosphorus, nitrogen, and organic sediment. The individual process equations which together comprise the state variable equations are also described herein. A parameter list (Table A1) describes each of the parameters used in the process equations and the values used in running the stand-alone version.

2. The macrophyte process equations correspond to those given in the main body of this report (although several variable names have been changed in this version of the model). Equations for the other six state variables contain terms reflecting the impacts of macrophyte processes on other components of aquatic ecosystems. This stand-alone version of the model is appropriate for implementation on a microcomputer.

3. There are some differences between the stand-alone version of the model and that recommended for CE-QUAL-R1. For the stand-alone version, (a) it was assumed that macrophyte production was not nutrient limited, (b) contributions to nutrients from macrophyte respiration were not included, and (c) contributions to nutrients from macrophyte nonpredatory mortality are included. Additionally, CE-QUAL-R1 does not include harvesting as the stand-alone version does.

- Ikusima, I. 1965. "Ecological Studies on the Productivity of Aquatic Plant Communities. I. Measurement of Photosynthetic Activity," Botanical Magazine of Tokyo, Vol 78, pp 202-211.
- Jewell, W. J. 1971. "Aquatic Weed Decay: Dissolved Oxygen Utilization and Nitrogen and Phosphorus Regeneration," Journal of Water Pollution Control Federation, Vol 43, pp 1457-1467.
- McGahee, C. F., and Davis, G. J. 1971. "Photosynthesis and Respiration in *Myriophyllum spicatum* L. as Related to Salinity," Limnology and Oceanography, Vol 16, pp 826-829.
- Miller, A. 1981. "Prediction of *Hydrilla* Growth and Biomass for Mechanical Harvesting Operations," Proceedings, 15th Annual Meeting, Aquatic Plant Control Research Planning and Operations Review, Miscellaneous Paper A-81-3, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.
- Nichols, D. S., and Keeney, D. R. 1976. "Nitrogen Nutrition of *Myriophyllum spicatum*: Variation of Plant Tissue Nitrogen Concentration with Season and Site in Lake Wingra," Freshwater Biology, Vol 6, pp 137-144.
- Olah, J. 1972. "Leaching, Colonization and Stabilization During Detritus Formation," Mem. Ist. Ital. Idrobiol., Vol 29, pp 105-127.
- Otsuki, A., and Hanya, T. 1972. "Production of Dissolved Organic Matter from Dead Green Algal Cells. I. Aerobic Microbial Decomposition," Limnology and Oceanography, Vol 17, pp 248-257.
- Stanley, R. A., and Naylor, A. W. 1972. "Photosynthesis in Eurasian Water-milfoil (*Myriophyllum spicatum* L.)," Plant Physiology, Vol 50, pp 149-151.
- Steele, J. H. 1962. "Environmental Control of Photosynthesis in the Sea," Limnology and Oceanography, Vol 7, pp 137-150.
- Strickland, J. D. H. 1960. "Measuring the Production of Marine Phytoplankton," Bulletin of the Fishery Research Board of Canada, Vol 122, 172 pp.
- Thornton, K. W., and Lessem, A. S. 1978. "A Temperature Algorithm for Modifying Biological Rates," Transactions of the American Fishery Society, Vol 107, pp 284-287.
- Van, T. K., Haller, W. T., and Bowes, G. 1976. "Comparison of the Photosynthetic Characteristics of Three Submersed Aquatic Plants," Plant Physiology, Vol 58, pp 761-768.
- Wetzel, R. G., and Manny, B. A. 1975. "Secretion of Dissolved Organic Carbon and Nitrogen by Aquatic Macrophytes," Verh. Internat. Verein. Limnol., Vol 18, pp 162-170.
- Wile, I. 1978. "Environmental Effects of Mechanical Harvesting," Journal of Aquatic Plant Management, Vol 16, pp 14-20.

Brylinsky, M., and Mann, K. H. 1973. "An Analysis of Factors Governing Productivity in Lakes and Reservoirs," Limnology and Oceanography, Vol 18, pp 1-14.

Carignan, R., and Kalff, J. 1980. "Phosphorus Sources for Aquatic Weeds: Water or Sediments?" Science, Vol 207, pp 987-989.

Carpenter, S. R. 1976. Some Environmental Impacts of Mechanical Harvesting of Nuisance Submersed Vascular Plants, Unpublished M.S. Thesis, University of Wisconsin.

Carpenter, S. R. 1980. "Enrichment of Lake Wingra, Wisconsin, by Submersed Macrophyte Decay," Ecology, Vol 6, pp 1145-1155.

de la Cruz, A. A., and Gabriel, B. C. 1974. "Caloric, Elemental, and Nutritive Changes in Decomposing *Juncus roemerianus* Leaves," Ecology, Vol 55, pp 882-886.

DeMarte, J. A., and Hartman, R. T. 1974. "Studies on Absorption of P, Fe, and Ca by Water Milfoil (*Myriophyllum exalbescent*, Fernald)," Ecology, Vol 55, pp 188-194.

Environmental Laboratory. 1982. "CE-QUAL-R1: A Numerical One-Dimensional Model of Reservoir Water Quality; A User's Manual," Instruction Report E-82-1 (Revised Edition; Supersedes Instruction Report E-82-1 dated April 1982), US Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Fitzgerald, G. P. 1964. "The Effect of Algae on BOD Measurements," National Pollution Control Federation Journal, Vol 36, pp 1524-1542.

Godshalk, G. L., and Wetzel, R. G. 1978. "Decomposition of Aquatic Angiosperms. I. Dissolved Components," Aquatic Botany, Vol 5, pp 281-300.

Hanlon, R. D. G. 1972. "The Breakdown and Decomposition of Allochthonous and Autochthonous Plant Litter in an Oligotrophic Lake," Hydrobiologia, Vol 88, pp 218-288.

Hargrave, B. T. 1972. "Aerobic Decomposition of Sediment and Detritus as a Function of Particle Surface Area and Organic Content," Limnology and Oceanography, Vol 17, pp 583-596.

Harrison, P. G., and Mann, K. H. 1975. "Detritus Formation From Eelgrass (*Zostera marina* L.): The Relative Effects of Fragmentation, Leaching and Decay," Limnology and Oceanography, Vol 20, pp 924-935.

Healey, F. P. 1976. "Ammonium and Urea Uptake by Some Freshwater Algae," Canadian Journal of Botany, Vol 55, pp 61-69.

Healey, F. P., and Hendzel, L. L. 1975. "Effect of Phosphorus Deficiency on Two Algae Growing in Chemostats," Journal of Phycology, Vol 11, pp 303-309.

Recommendations

31. It is recommended that the model for submersed aquatic plants described in this report be incorporated in the CE-QUAL-R1 model with due consideration of the following points:

- a. The light response function should permit representation of photoinhibition (this same algorithm should be used for algae in CE-QUAL-R1).
- b. Because nutrients are an explicit part of the photosynthesis algorithm, limitation should be based on the Monod function for the nutrient shown to be limiting using threshold ratios.
- c. The spatial relationships of the rooted zone of macrophytes to the model layers should be accounted for based on the intersection of model layers with the reservoir bottom, creating a two-dimensional array of cells for macrophyte computations; the macrophytes should be apportioned into the vertical layers based on cell-by-cell computations and a comparison with a user-specified maximum macrophyte density in each cell; this algorithm can also be used to determine the biomass of macrophytes cut by a mechanical harvester set at a particular depth.
- d. Chemical control can be modeled using dose-response relationships.

References

- Adams, M. S., Titus, J., and McCracken, M. 1974. "Depth Distribution of Photosynthetic Activity in a *Myriophyllum spicatum* Community in Lake Wingra," Limnology and Oceanography, Vol 19, No. 3, pp 377-389.
- Barko, J. W., and Smart, R. M. 1980. "Mobilization of Sediment Phosphorus by Submersed Freshwater Macrophytes," Freshwater Biology, Vol 10, pp 229-238.
- Barko, J. W., Smart, R. M., Hardin, D. G., and Matthews, M. S. 1980. "Growth and Metabolism of Three Introduced Submersed Plant Species in Relation to the Influences of Temperature and Light," Technical Report A-80-1, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.
- Best, M. D., and Mantai, K. E. 1978. "Growth of *Myriophyllum*: Sediment or Lake Water as the Source of Nitrogen and Phosphorus?" Ecology, Vol 59, pp 75-80.
- Bole, J. B., and Allan, J. R. 1978. "Uptake of Phosphorus from Sediment by Plants, *Myriophyllum spicatum* and *Hydrilla verticillata*," Water Research, Vol 12, pp 353-358.
- Bowes, G., Van, T. K., Ganard, L. A., and Haller, W. T. 1977. "Adaptation to Low Light Levels by *Hydrilla*," Journal of Aquatic Plant Management, Vol 15, pp 32-35.

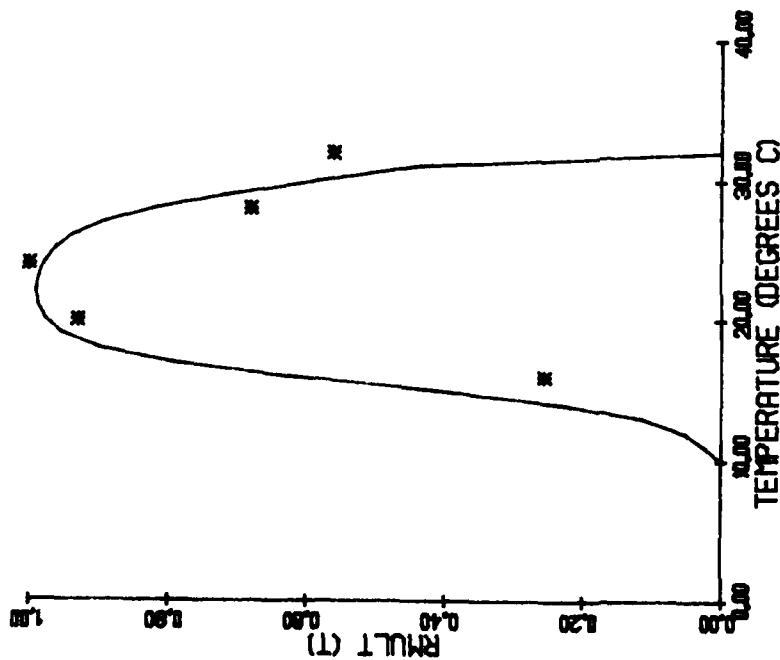


Figure 5. Process validation plot using the Thornton and Lessem (1978) equation, RMULT, as a temperature rate multiplier to predict the effect of temperature on photosynthetic rate. Asterisks represent normalized experimental results from Barko et al. (1980). Process parameter values are given in text

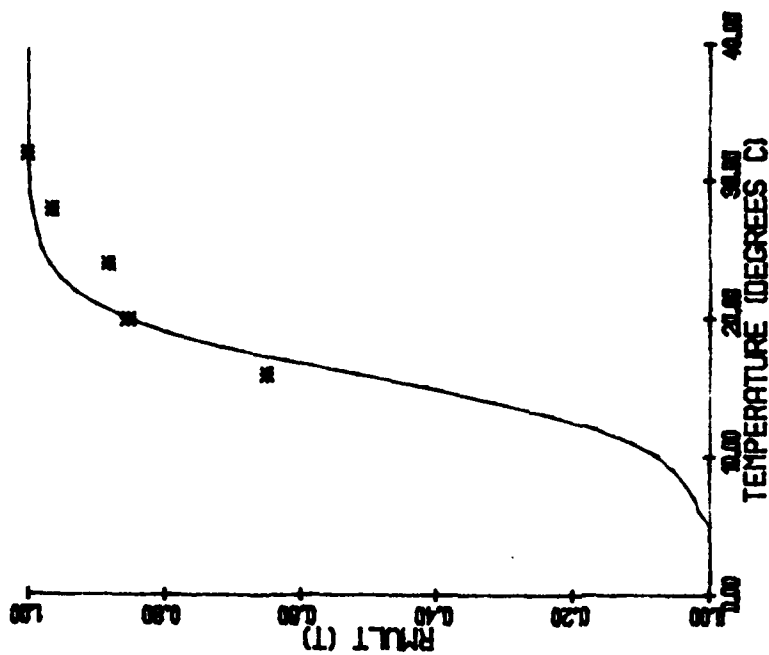


Figure 6. Process validation plot using the rising limb of the Thornton and Lessem (1978) equation, RMULT, as a temperature rate multiplier to predict the effect of temperature on dark respiration rate. Asterisks represent the normalized experimental results from Barko et al. (1980) for *H. verticillata*. Process parameter values are given in text

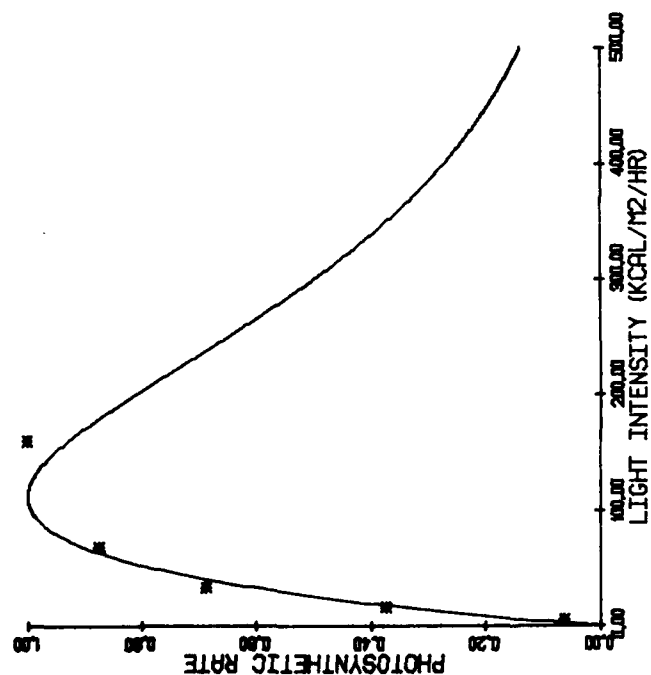


Figure 3. Process validation plot using Steele's (1962) equation to represent the photosynthetic light intensity response of *M. spicatum*. Asterisks represent normalized experimental results from Van, Haller, and Bowes (1976). Process parameter values are given in text

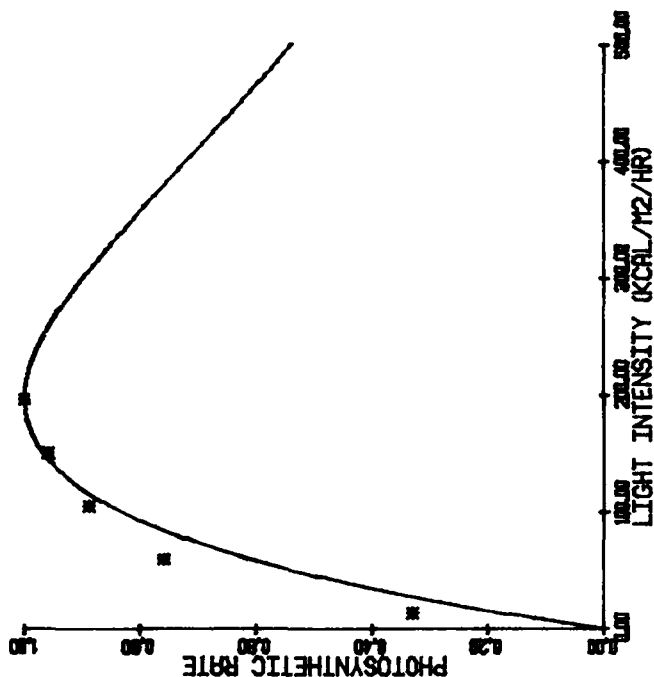


Figure 4. Process validation plot using Steele's (1962) equation to represent the photosynthetic light intensity response of *H. verticillata*. Asterisks represent normalized experimental results from Barko et al. (1980). Process parameter values are given in text

Depending on how the chemical control program is implemented, the macrophyte mass killed can be transferred as appropriate to other model compartments (detritus, sediment, dissolved organic matter).

Process Validation

27. Select process equations included in the proposed macrophyte sub-model have been validated based on experimental results from the literature and published experimental results performed at the US Army Engineer Waterways Experiment Station by Dr. John Barko and colleagues. Data on two macrophyte species of particular interest to the Corps were used in this validation procedure, *M. spicatum* and *H. verticillata*. Results of validating several specific equations in the macrophyte model are discussed in the following paragraphs.

28. The equation used to represent the photosynthetic light response is that of Steele (1962) (see Equation 5 and Appendix B). Figures 3 and 4 demonstrate that this equation fits experimental data from Van, Haller, and Bowes (1976) for *M. spicatum* and from Barko et al. (1980) for *H. verticillata*. The parameter PISAT, which describes the saturating light intensity for photosynthesis, was set at 112 and 196 kcal m⁻² hr⁻¹, respectively, for *M. spicatum* and *H. verticillata* (Appendix B). Photoinhibition at high light intensities can also be predicted using this equation. Although this type of response of these two species to high light intensities has not been observed, other species demonstrate photoinhibition which could be significant during reservoir drawdown.

29. The effect of temperature on photosynthesis is represented using the equation of Thornton and Lessem (1978) (Equation 3). Validation of this equation for *H. verticillata*, based on results of Barko et al. (1980), is demonstrated in Figure 5. The parameter values used in this equation are as follows: T1 = 10°C, T2 = 20°C, T3 = 24°C, T4 = 32°C, K1 = 0.01, K2 = 0.98, K3 = 0.98, and K4 = 0.30 (Appendices A and B).

30. Validation of the equation representing dark respiration (Equation 6) is represented in Figure 6 for *H. verticillata*. The parameter values used are as follows: T1 = 5°C, T2 = 25°C, K1 = 0.01, and K2 = 0.98 (Appendix B).

The index J ranges from 1 (top layer) up to a user-specified value indicating the maximum number of layers in which macrophytes can occur (actually, the maximum rooting depth in metres). If all the mass in that column can be contained in the bottommost cell, it is placed there. Otherwise, Equation 9 is iterated (i.e., the value of J is increased sequentially) until the calculated total macrophyte mass for that column is apportioned among cells in that column, such that the mass in each cell is less than or equal to the maximum calculated with Equation 9. The total macrophyte mass is then calculated for each model layer by summation, and for the entire reservoir.

Management Control Processes

25. In addition to ecological processes, the model can also simulate management control processes including mechanical harvesting and chemical control of the plants. Macrophyte mass removed by mechanical harvesting is a function of plant rooting depth and mass density as well as the cutting depth of the mechanical harvester. Having determined macrophyte biomass in each model layer, the amount cut (MBIOCUT) by a mechanical harvester set at a particular cutting depth (CUTZ) can be calculated by summation. If the cutting depth falls between layer boundaries, then an appropriate fraction of the macrophyte mass in that layer can be removed since mass is assumed to be distributed homogeneously within layers.

26. Chemical control is a function of the following dose-response curve for the herbicide used:

$$MCHEM(I) = MACRO(I) * CHEM / (LC50 + CHEM) \quad (10)$$

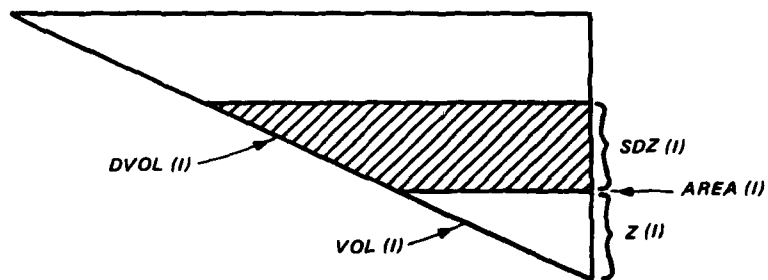
where

MCHEM(I) = macrophyte biomass killed in layer I, g

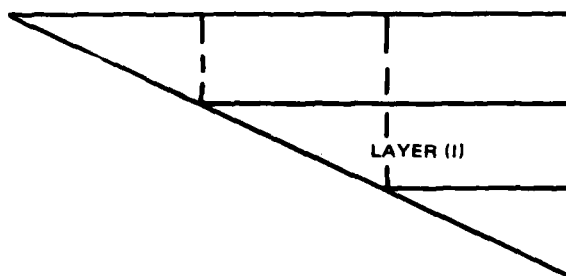
MACRO(I) = total macrophyte biomass in layer I, g

CHEM = user-specified ambient environmental concentration of herbicide applied, $\mu\text{g l}^{-1}$

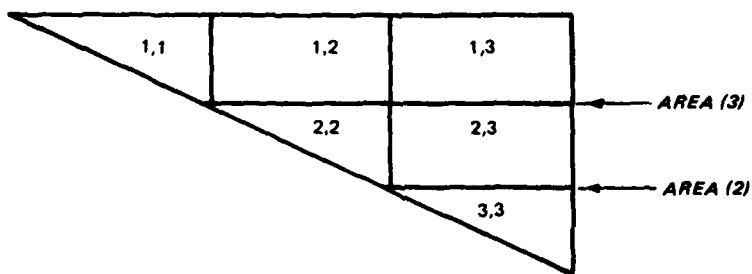
LC50 = user-specified herbicide concentration which will kill 50 percent of the macrophytes, $\mu\text{g l}^{-1}$



a. VARIABLE LAYERS



b. VERTICAL SEGMENTS



c. CELL VOLUMES

Figure 2. Model structure for macrophyte distribution

the Ith layer. The actual volume of the Ith layer, DVOL(I), is calculated as the difference between VOL(I+1) and VOL(I). Both volume and area are typically represented as power functions of elevation.

23. Using this scheme, a series of vertical segments or columns can be superimposed at the points at which boundary layers intersect the reservoir bottom (Figure 2b), creating a series of two-dimensional cells for macrophyte computations (Figure 2c). To simplify the computational sequence, these cells are numbered from the reservoir surface down, and from upstream toward the dam. A given cell is indexed (i,j) with i referring to row position and j to column. Because each of the layers in the model representation of a reservoir is extremely long and thin, the bottom surface area in which macrophytes root can be approximated as the difference AREA(I+1) - AREA(I). Similarly, the volume of each computational cell can be approximated as this bottom surface area times the thickness (SDZ) of the layer in which that cell occurs. These bottom areas and cell volumes are used in macrophyte computations as described in the following paragraph.

24. Macrophytes are associated with the bottom sediments in which they are rooted and with the overlying water column. In order to determine how macrophyte mass is apportioned among the cells in a given vertical column, the assumption is made that the volumetric density of macrophyte dry mass cannot exceed a user-specified maximum value (PLDENS, g m^{-3}). At each model time step, the macrophyte differential equation (Equation 1) is solved on a cell-by-cell basis using a simple Euler procedure and the mass is calculated at the previous time step as an initial value. Then macrophyte mass is summed over all cells in a given column. Beginning with the bottommost cell (i.e., the one nearest the sediment), this summed mass is apportioned among cells by comparing it with the maximum mass which each cell can contain. For cells in the Ith column, this maximum is calculated as

$$\text{DATA}(J,I) = \text{PLDENS} * \text{SDZ}(J) * (\text{AREA}(I+1) - \text{AREA}(I)) \quad (9)$$

where

DATA(J,I) = maximum macrophyte mass which can be contained in the cell in layer J and column I, g

PLDENS = user-specified maximum macrophyte volumetric density, g m^{-3}

SDZ(J) = thickness of Jth model layer, m

AREA(I) = bottom surface area at layer I, m^2

coefficients are involved. In a similar manner, grazing represents a direct transfer of mass to fish, without conversion. As a consequence of nonpredatory mortality, macrophyte biomass is transferred to dissolved organic matter, detritus, and sediment compartments. The "dead" biomass is apportioned between the three receiver compartments based on user-specified coefficients.

20. Included in Appendix A is a stand-alone version of the macrophyte model which was used in validating the various process equations just discussed. In addition to containing the equations describing macrophyte physiological processes (Equations 1-8), this version of the model also contains equations for oxygen, particulate organic matter, dissolved organic matter, phosphorus, nitrogen, and sediment. This model thus illustrates the way in which macrophyte terms enter into equations for other water quality constituents included in CE-QUAL-R1. In Appendix B, representative values for the parameters included in Equations 1-8 of the macrophyte model (as defined in Appendix A) are listed, based on research on two macrophyte species of particular interest, *Myriophyllum spicatum* and *Hydrilla verticillata*. CE-QUAL-R1-related parameters and coefficient values are also listed in Appendix B.

Spatial Relationships

21. In order to describe vertical growth of macrophytes in a one-dimensional, variable-layer model like CE-QUAL-R1, it was necessary to devise a means of geometrically segmenting the model into a matrix of rows (layers) and columns. This matrix defines the volume of each segment and the proximity of one segment to another. A description of how the matrix can be incorporated into the CE-QUAL-R1 model follows.

22. CE-QUAL-R1 is a one-dimensional model with multiple layers. Thermal energy and materials are assumed to be uniformly distributed within each model layer. Reservoir morphometry is represented in the model by a variable-layer approach (i.e., layer dimensions vary over time based on inflows and outflows and on user-specified morphometric relationships of area and volume to elevation above the reservoir bottom). Relationships among elevation, area, and volume are depicted in Figure 2a. A given layer (numbered I, from the bottom up) is specified as being Z(I) metres above the bottom and SDZ(I) metres thick. The area of the Ith layer, AREA(I), is defined at the lower boundary of that layer. A volume, VOL(I), is also defined up to the lower surface of

7

calculated as the product of the two temperature limitation functions, RMULT1 and RMULT2 (Equation 3), times a user-specified maximum fish grazing rate, times a Monod function similar in form to Equation 4. In this fish-grazing limitation function, the role of C (Equation 4) is played by the sum, over all types of food (including macrophytes) ingested by fish, of products of a user-specified preference factor for that food type and the concentration of that food type. For this grazing function, $K_{1/2}$ (in Equation 4) would again be a user-specified half-saturation coefficient for fish grazing. The reader should consult the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982) for further details. An additional preference factor would need to be included in the model, specifying the fractional preference of fish for macrophytes.

Interactions with other compartments in CE-QUAL-R1

18. As depicted in Figure 1, those macrophyte processes discussed above also impact a variety of other compartments in CE-QUAL-R1. Thus, corresponding to the process equations given above (Equations 1-8), terms will need to be added to or subtracted from other equations in the model. These terms represent the addition or removal of mass to or from other compartments in the modeled reservoir. These terms will be briefly described here. Although the actual equations will not be provided, they correspond exactly to the form of the equations listed previously.

19. As a result of macrophyte photosynthetic processes, oxygen is evolved. This is modeled as an "equivalent oxygen concentration," calculated as the product at the gross production rate of concentration and a user-specified oxygen-to-biomass stoichiometric coefficient, which is added directly to the oxygen differential equation. Similarly, dark respiration removes oxygen. This removal, a subtraction from the oxygen equation, is calculated as the product of the dark respiration rate of concentration and another user-specified stoichiometric coefficient. Gross production and respiration also result in the uptake and release, respectively, of nutrients (N, P, C) from and to the water column and sediments (Figure 1). These transfers are calculated as the product of the production and respiration rates of concentration and user-specified nutrient-to-biomass stoichiometric coefficients. Photorespiration represents a direct addition of mass to the ammonia-nitrogen, phosphorus, and dissolved organic matter compartments; no conversion

mathematically using only the rising limb of the temperature equation of Thornton and Lessem (1978) (Equation 3):

$$MRESP = MKRESP * RMULT1(T) \quad (6)$$

where

MRESP = dark respiration rate, day⁻¹

MKRESP = user-specified maximum dark respiration rate, day⁻¹

15. Photorespiration. Photorespiration or excretion is important because it results in the phenomenon known as "nutrient pumping," whereby nutrients are transferred from bottom sediments to water. This process also increases the amount of organic matter dissolved in the water column. Excretion is a function of light intensity. Under conditions of very high or very low light intensities, the rate of extracellular release increases. Mathematically this is represented as

$$MEXCR = (1 - XLIML) * MKEXCR \quad (7)$$

where

MEXCR = excretion rate, day⁻¹

MKEXCR = user-specified maximum excretion rate, day⁻¹

16. Nonpredatory mortality. Nonpredatory mortality is temperature-dependent when the change in temperature (increase or decrease) over a 7-day period exceeds a critical maximum temperature TMPMAX. Therefore, if $|TMPTUR(1) - TMPTUR(7)| > TMPMAX$:

$$MMORT = MKMORT \quad (8)$$

where

TMPTUR(1) and TMPTUR(7) = water temperature over 7-day period, °C

TMPMAX = maximum temperature change, °C

MMORT = nonpredatory mortality rate, day⁻¹

MKMORT = user-specified maximum nonpredatory mortality rate, day⁻¹

17. Grazing. Grazing of macrophytes by fish is modeled with the same type of grazing function as used in CE-QUAL-R1. Thus, the grazing rate is

compartments representing sediment nitrogen and phosphorus; therefore, limitation of nutrients obtained through the roots can occur, although this is rare in nature. This process is most important in allowing "nutrient pumping" from the sediments into the water column.

12. In some cases where nutrient concentrations in the water are high, it becomes advantageous for the plant to draw nutrients from the water column. In water with a phosphorus concentration of 2.0 mg l^{-1} , characteristic of eutrophic reservoirs, *Myriophyllum spicatum* took phosphorus from the water column (Bole and Allan 1978). This is modeled using a species-specific parameter to indicate the water concentration above which nutrients are taken from the water column. Whenever the water column concentration of nitrogen or phosphorus equals or exceeds this user-specified concentration, it is the water concentration of that nutrient which is entered into the Monod equation (Equation 4). Otherwise, it is the sediment concentration of nitrogen or phosphorus which is used in Equation 4.

13. Light limitation is represented using Steele's equation (1962):

$$XLIML = \left(\frac{0.5 * SWSA}{PISAT} \right) \exp \left[1 - \left(\frac{0.5 * SWSA}{PISAT} \right) \right] \quad (5)$$

where

SWSA = average irradiance for a specific model layer, $\text{kcal m}^{-2} \text{ hr}^{-1}$
(calculated in Subroutine HEAT in CE-QUAL-R1)

PISAT = user-specified irradiance level at which the photosynthetic rate is saturated (i.e., occurs at maximum rate), $\text{kcal m}^{-2} \text{ hr}^{-1}$

The coefficient value 0.5 is used in Steele's equation to represent the fraction of total irradiance that is photosynthetically active radiation (PAR). PAR is in the range of 400 to 700 nm. Steele's equation can predict photoinhibition of photosynthesis at high light intensities, above the level specified by PISAT. Solar radiation is distributed vertically in the water column in CE-QUAL-R1 based upon the extinction coefficient for water. Light is also attenuated by self-shading by algae, zooplankton, detritus, and suspended solids. An additional self-shading coefficient should be included in the model to account for the effect of macrophyte biomass on light attenuation.

14. Dark respiration. Dark respiration is a function of temperature. As with other respiratory rates in CE-QUAL-R1, it is represented

State Variable Equations*

Macrophyte

$$\dot{\text{MACRO}} = \text{MPROD} - \text{MRESP} - \text{MEXCR} - \text{MMORT} - \text{MHVST}$$

macrophyte = photosynthesis - dark respiration - excretion (photo-respiration) - mortality - harvesting

Oxygen

$$\dot{\text{OXYGEN}} = \text{OTST} + \text{OMAC} - \text{ANIT} - \text{OPDK} - \text{ODDK} - \text{OSDK}$$

Oxygen = oxygen saturation + contribution from macrophytes

- equivalent loss from nitrogen decay - equivalent loss from POM decay

- equivalent loss from DOM decay - equivalent loss from sediment decay

Particulate organic matter

$$\dot{\text{POM}} = \text{PMAC} - \text{PDK} - \text{PSTL}$$

POM = contribution from macrophyte mortality and harvesting

- loss from POM decay - loss from settling

Dissolved organic matter

$$\dot{\text{DOM}} = \text{DMAC} + \text{DEXCR} + \text{DDK} - \text{DBAC}$$

DOM = contribution from macrophyte mortality and harvesting + contribution from macrophyte excretion + contribution from POM decay - loss from bacterial respiration

Phosphorus (water column)

$$\dot{\text{PO4}} = \text{FMAC} + \text{FDK} + \text{FEXCR} - \text{FSINK}$$

PO4 = contribution from macrophyte mortality and harvesting + contribution from decay of POM and sediments + contribution from macrophyte excretion - loss to algal production

* Each equation represents the time rate of change of the state variable for a model layer. The units of MACRO are grams per square metre per day per model layer. The units of all other state variables are grams per square metre per day per metre of model layer.

Nitrogen (water column)

$$\dot{N} = NMAC + NDK + NEXCR - NSINK$$

N = contribution from macrophyte mortality and harvesting
+ contribution from decay of POM and sediments
+ contribution from macrophyte excretion - loss to algal production

Organic sediment

$$\dot{SED} = SMAC - SDK$$

SED = contribution from macrophyte mortality and harvesting
- loss from sediment decay

Process Equations

Macrophyte

$$MPROD = PMAX * RMULT1(T) * RMULT2(T) * LIGHT * MACRO$$

where

PMAX = maximum photosynthetic rate, day⁻¹

RMULT1(T) = temperature limitation function, unitless

RMULT2(T) = temperature limitation function, unitless

T = ambient water temperature, °C

LIGHT = light limitation function, unitless

MACRO = macrophyte biomass, g m⁻²

$$LIGHT = \frac{e}{\epsilon(Z2-Z1)} \left\{ e^{\left[\frac{(-0.5 \cdot IO)}{ISAT} e^{-\epsilon Z2} \right]} - e^{\left[\frac{(-0.5 \cdot IO)}{ISAT} e^{-\epsilon Z1} \right]} \right\}$$

where

ϵ = extinction coefficient

Z2 = depth at the bottom of the simulated section, m

Z1 = depth at the top of the simulated section, m

IO = irradiance at the water surface, kcal m⁻² sec⁻¹

ISAT = saturating irradiance for photosynthesis, kcal m⁻² sec⁻¹

$$MRESP = KRESP * RMULT1(T) * MACRO$$

where

KRESP = user-specified maximum respiration rate, $g\ g^{-1}\ day^{-1}$

$$MEXCR = KEXCR * (1-LIGHT) * MACRO$$

where

KEXCR = user-specified maximum excretion rate, $g\ g^{-1}\ day^{-1}$

If, $|TMPTUR(1) - TMPTUR(7)|$ is greater than TMPMAX, then

$$MMORT = KMORT * MACRO$$

where

KMORT = nonpredatory mortality rate, $g\ g^{-1}\ day^{-1}$

TMPMAX = critical maximum temperature difference over a 7-day period, °C

TMPTUR(1) and TMPTUR(7) = water temperatures over a 7-day period, °C

$$MHVST = CHEM * MACRO$$

where

CHEM = rate of die-off of macrophyte dependent upon type of chemical used, $g\ g^{-1}\ day^{-1}$

NOTE: Mechanical harvesting is calculated outside the differential equation as follows:

$$MWH + MACRO = MHT$$

$$Z - MHT = TPLT$$

$$CUTZ - TPLT = MCUT$$

$$MWH + MCUT = MBIOCUT$$

where

MWH = species-specific weight-to-height ratio, g m^{-1}
MHT = macrophyte height, m
Z = depth of water column, m
TPLT = top of plant, m
CUTZ = cutting depth of mechanical harvester, m
MCUT = amount of macrophyte cut, m
MBIOCUT = biomass of macrophyte cut, g m^{-2}

Oxygen

OTST = $(14.6 * \exp(-(0.027767 - 0.00027 * T + 0.000002 * T * T) * T)) * Z$
OMAC = $(\text{OMACEQ1} * \text{MPROD}) - (\text{OMACEQ2} * \text{MRESP})$
ANIT = $\text{ONEQ} * \text{NMAC}$
OPDK = $\text{OPEQ} * \text{PDK}$
ODDK = $\text{ODEQ} * \text{DDK}$
OSDK = $\text{OSEQ} * \text{SDK}$

Particulate organic matter

PMAC = $(\text{MMORT} * \text{M1}) + (\text{MHVST} * \text{H1})$
PDK = $\text{KPOM} * \text{POM} * \text{RMULT1}(T)$
PSTL = $(\text{PMSTL} * \text{MMORT}) + (\text{PHSTL} * \text{MHVST})$
KPOM = $0.01192 * 1/\text{NTC}(2) + 0.00672$

Dissolved organic matter

DMAC = $(\text{MMORT} * \text{M2}) + (\text{MHVST} * \text{H2})$
DEXCR = $\text{MEXCR} * \text{E2}$
DDK = $\text{PDK} * \text{P2}$
DBAC = $\text{KDOM} * \text{DOM} * \text{RMULT1}(T)$
KDOM = $0.024 * 1/\text{NTC}(3) + 0.0192$

Phosphorus

FMAC = $(\text{MMORT} * \text{M3}) + (\text{MHVST} * \text{H3})$
FDK = $(\text{PDK} * \text{P3}) + (\text{SDK} * \text{S3})$
FEXCR = $\text{MEXCR} * \text{E3}$
FSINK = $\text{photoplankton biomass} * \text{FRS}$

Nitrogen

$$\text{NMAC} = (\text{MMORT} * \text{M4}) + (\text{MHVST} * \text{H4})$$

$$\text{NDK} = (\text{PDK} * \text{P4}) + (\text{SDK} * \text{S4})$$

$$\text{NEXCR} = \text{MEXCR} * \text{E4}$$

$$\text{NSINK} = \text{photoplankton biomass} * \text{NRS}$$

Sediments

$$\text{SMAC} = (\text{MMORT} * \text{M5}) + (\text{MHVST} * \text{H5})$$

$$\text{SDK} = \text{KSED} * \text{SED} * \text{RMULT1(T)}$$

$$\text{KSED} = 0.00519 * 1/\text{NTC}(4) + 0.00346$$

Table A1

Stand-Alone Version Macrophyte Model Parameter List

Parameter	Parameter Description	Value	Reference
Z	Depth of water column, m	Specified by user	
CHDA	Chemical dependent rate of macrophyte die-off, $\text{g g}^{-1} \text{ day}^{-1}$	Specified by user	
CUTZ	Cutting depth of mechanical cutter, m	Specified by user	
TEMPAX	Critical maximum temperature difference for nonpredatory mortality, $^{\circ}\text{C}$	5	Boylan, unpublished data
ISAT	Saturating light intensity for photosynthesis, $\text{kcal m}^{-2} \text{ sec}^{-1}$	112 196	Van, Haller, and Boves (1976) Barko et al. (1980)
KEXCR	Excretion rate for macrophyte, $\text{g g}^{-1} \text{ day}^{-1}$	0.023 0.017	Stanley and Naylor (1972) Boves et al. (1977)
EMORT	Mortality rate for macrophyte, $\text{g g}^{-1} \text{ day}^{-1}$	0.001	Calibrated
KSED	Decay rate for sediment, $\text{g g}^{-1} \text{ day}^{-1}$	0.001 - 0.015	Hargrave (1972)
KPOM	Decay rate for POM, $\text{g g}^{-1} \text{ day}^{-1}$	0.007 - 0.06 dead mixed algae 0.002 - 0.007 Potomogeton	Fitzgerald (1964) Hanlon (1972)
KRESP	Respiration rate for macrophyte, $\text{g g}^{-1} \text{ day}^{-1}$	0.027 0.016 - 0.039	Boves et al. (1977) McGahee and Davis (1971)
KDOM	Decay rate (bacterial respiration) for DOM, $\text{g g}^{-1} \text{ day}^{-1}$	0.238	Carpenter (1980)
PMAX	Maximum photosynthetic rate, $\text{g g}^{-1} \text{ day}^{-1}$	0.48 - 0.6 0.02 - 0.6	Van, Haller, and Boves (1976); Ikusima (1965) Adam, Titus, and McCracken (1974)
OMEQ	Oxygen equivalent for nitrogen decay or mineralization, unitless	3.43	Calculated
OPEQ	Oxygen equivalent for POM mineralization or decay, unitless	1.3	Jewell (1971)
ODEQ	Oxygen equivalent for DOM mineralization or decay, unitless	1.3	Jewell (1971)
OSEQ	Oxygen equivalent for sediment mineralization or decay, unitless	1.3	Jewell (1971)

(Continued)

(Sheet 1 of 4)

Table A1 (Continued)

Parameter	Parameter Description	Value	Reference
OMACEQ	Oxygen equivalent for macrophyte photosynthesis and respiration, unitless	1.0 1.2	Brylinsky and Mann (1973) Strickland (1960)
PMSTL	Mortality fraction of POM that sediments	20 to 50%	Calibrated
PMSTL	Harvested fraction of POM that sediments	10 to 40%	Calibrated
NBS	Nitrogen uptake rate by phytoplankton, $g\ g^{-1}\ day^{-1}$	0.012 to 0.035	Healey (1976)
PBS	Phosphorus uptake rate by phytoplankton, $g\ g^{-1}\ day^{-1}$	0.3 to 0.6	Healey and Hendzel (1975)
M1	Fraction of dying macrophyte that goes to POM, unitless	29%	Godshalk and Wetzel (1978)
M2	Fraction of dying macrophyte that goes to DOM, unitless	1 to 10%	Wetzel and Manny (1975)
M3	Fraction of dying macrophyte that goes to phosphorus, unitless	0.13 to 0.60%	Wile (1978)
M4	Fraction of dying macrophyte that goes to nitrogen, unitless	1.2 to 2.8%	Wile (1978)
M5	Fraction of dying macrophyte that goes to sediment, unitless	18%	Carpenter (1976)
H1	Fraction of harvested macrophyte that goes to POM, unitless	Specified by user; dependent on harvesting method	
H2	Fraction of harvested macrophyte that goes to DOM, unitless		
H3	Fraction of harvested macrophyte that goes to phosphorus, unitless		
H4	Fraction of harvested macrophyte that goes to nitrogen, unitless		
H5	Fraction of harvested macrophyte that goes to sediment, unitless		

(Continued)

(Sheet 2 of 4)

Table A1 (Continued)

Parameter	Parameter Description	Value	Reference
E2	Fraction of excretion that goes to phosphorus, unitless	4 to 6% <i>Egeria densa</i> 7 to 29% <i>Hydrilla verticillata</i> 1 to 4% <i>Myriophyllum spicatum</i>	Barbo and Smart (1980)
E3	Fraction of excretion that goes to nitrogen, unitless	11%	Wetzel and Manny (1975)
E4	Fraction of excretion that goes to DOM, unitless	1 to 10%	Wetzel and Manny (1975)
P2	Fraction of decaying POM that goes to DOM, unitless	15 to 46%	Godshalk and Wetzel (1978)
P3	Fraction of decaying POM that goes to phosphorus, unitless	0.12%	de la Cruz and Gabriel (1974)
P4	Fraction of decaying POM that goes to nitrogen, unitless	0.40%	de la Cruz and Gabriel (1974)
S3	Fraction of decaying sediment that goes to phosphorus, unitless	0.10 to 0.15%	Calibrated
S4	Fraction of decaying sediment that goes to nitrogen, unitless	0.40 to 1.0%	Calibrated
MACRO	Initial macrophyte biomass, $g\ m^{-2}$	Specified by user	
OXY	Initial oxygen concentration, $g\ m^{-3}$		
POM	Initial POM concentration, $g\ m^{-3}$		
DOM	Initial DOM concentration, $g\ m^{-3}$		
P	Initial phosphorus concentration, $g\ m^{-3}$		
N	Initial nitrogen concentration, $g\ m^{-3}$		
SED	Initial sediment concentration, $g\ m^{-3}$		
K1	Temperature rate factor for photosynthesis and respiration at $T = T_1$	0.01	Calibrated
K2	Temperature rate factor for photosynthesis and respiration at $T = T_2$	0.98	Calibrated

(Continued)

(Sheet 3 of 4)

Table A1 (Concluded)

Parameter	Parameter Description	Value	Reference
K3	Temperature rate factor for photosynthesis at $T = T_3$	0.98	Calibrated
K4	Temperature rate factor for photosynthesis at $T = T_4$	0.30	Calibrated
T1	Critical low temperature for photosynthesis and respiration, °C	10°C	Barko et al. (1980); Van, Haller and Boves (1976)
T2	Optimum low temperature for photosynthesis and respiration, °C	16°C 20°C	Van, Haller, and Boves (1976) Barko et al. (1980)
T3	Optimum high temperature for photosynthesis, °C	24°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis, °C	32°	Barko et al. (1980)
MMH	Species-specific weight-to-height ratio, g m ⁻¹	0.78 2.40	Boylan, unpublished data Miller (1981)
NTC(1)	Nitrogen to carbon ratio for macrophytes	0.03 to 0.08	Godshalk and Wetzel (1978)
NTC(2)	Nitrogen to carbon ratio for POM	0.05	Harrison and Mann (1975)
NTC(3)	Nitrogen to carbon ratio for DOM	0.09 to 0.16	Otsuki and Hanya (1972)
NTC(4)	Nitrogen to carbon ratio for sediments	0.06 to 0.16	Olah (1972)

APPENDIX B: MACROPHYTE MODEL PARAMETER LIST

Tabulated in Table B1 in this Appendix are values for specific parameters included in the state variable and process equations which comprise the macrophyte model proposed in the main body of this report (as intended for inclusion in CE-QUAL-R1). These values were either derived from published literature sources or established in the process validation studies described earlier. Most values tabulated here apply to one or two macrophyte species of interest, *Myriophyllum spicatum* or *Hydrilla verticillata*.

Table B1

Macrophyte Model Parameter List Recommended for CE-QUAL-R1

Parameter	Description	Species	Value	Converted Value	Reference
PISAT	Saturating light intensity for photosynthesis	<i>M. spicatum</i>	$600 \mu\text{E m}^{-2} \text{ sec}^{-1}$	$112 \text{ kcal m}^{-2} \text{ hr}^{-1}$	Van, Haller, and Boves (1976)
PISAT		<i>M. spicatum</i>	$1050 \mu\text{E m}^{-2} \text{ sec}^{-1}$	$196 \text{ kcal m}^{-2} \text{ hr}^{-1}$	Barko et al. (1980)
PISAT		<i>H. verticillata</i>	$600 \mu\text{E m}^{-2} \text{ sec}^{-1}$	$112 \text{ kcal m}^{-2} \text{ hr}^{-1}$	Van, Haller, and Boves (1976)
PLTMAX	Maximum photo-synthetic rate	<i>M. spicatum</i>	$3.3 \mu\text{mole CO}_2 \text{ mg chl}^{-1} \text{ hr}^{-1}$	$0.04 \text{ g g}^{-1} \text{ hr}^{-1}$	Van, Haller, and Boves (1976)
PLTMAX		<i>M. spicatum</i>	$0.8 - 4.6 \mu\text{mole CO}_2 \text{ mg chl}^{-1} \text{ hr}^{-1}$	$0.09 - 0.05 \text{ g g}^{-1} \text{ hr}^{-1}$	Adams, Titus, and McCracken (1974)
PLTMAX		<i>H. verticillata</i>	$4.6 \mu\text{mole CO}_2 \text{ mg chl}^{-1} \text{ hr}^{-1}$	$0.05 \text{ g g}^{-1} \text{ hr}^{-1}$	Van, Haller, and Boves (1976)
PLTMAX		<i>H. verticillata</i>	$5 \text{ mg CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$	$0.05 \text{ g g}^{-1} \text{ hr}^{-1}$	Ikusima (1965)
MKRESP	Dark respiration	<i>M. spicatum</i>	$2.5 \mu\text{mole CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$	$0.027 \text{ g g}^{-1} \text{ hr}^{-1}$	Boves et al. (1977)
MKRESP	Dark respiration	<i>H. verticillata</i>	$1.5 - 3.6 \mu\text{moles mg chl}^{-1} \text{ hr}^{-1}$	$0.016 - 0.039 \text{ g g}^{-1} \text{ hr}^{-1}$	McGahee and Davis (1971)
MKEXCR	Photorespiration rate	<i>M. spicatum</i>	$0.023 \text{ g g}^{-1} \text{ hr}^{-1}$	$0.023 \text{ g g}^{-1} \text{ hr}^{-1}$	Stanley and Naylor (1972)
MCMORT	Nonpredatory mortality rate			$0.001 \text{ g g}^{-1} \text{ hr}^{-1}$	Calibrated

(Continued)

(Sheet 1 of 5)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
TMPMAX	Maximum 7-day temperature change for non-predatory mortality			5°C	Boylen, unpublished data
T1	Critical low temperature for photosynthesis	<i>M. spicatum</i>	10°C	10°C	Van, Haller, and Boves (1976)
T1	Critical low temperature for photosynthesis	<i>H. verticillata</i>	10°C	10°C	Barko et al. (1980)
T2	Low optimum temperature for photosynthesis	<i>M. spicatum</i>	16°C	16°C	--
T2	Low optimum temperature for photosynthesis	<i>H. verticillata</i>	20°C	20°C	Barko et al. (1980)
T3	High optimum temperature for photosynthesis	<i>M. spicatum</i>	35°C	35°C	--
T3	High optimum temperature for photosynthesis	<i>H. verticillata</i>	24°C	24°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis	<i>M. spicatum</i>	44°C	44°C	Barko et al. (1980)
T4	Critical high temperature for photosynthesis	<i>H. verticillata</i>	32°C	32°C	Barko et al. (1980)

(Continued)

(Sheet 2 of 5)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
K1	Temperature rate multiplier for photosynthesis	<i>M. spicatum</i>	0.01	0.01	Calibrated
K1	Temperature rate multiplier for photosynthesis	<i>H. verticillata</i>	0.01	0.01	
K2		<i>M. spicatum</i>	0.98	0.98	
K2		<i>H. verticillata</i>	0.98	0.98	
K3		<i>M. spicatum</i>	0.98	0.98	
K3		<i>H. verticillata</i>	0.98	0.98	
K4		<i>M. spicatum</i>	0.28	0.28	
K4		<i>H. verticillata</i>	0.30	0.30	
T1	Critical low temperature for dark respiration	<i>M. spicatum</i>	5°C	5°C	
T1	Critical low temperature for dark respiration	<i>H. verticillata</i>	5°C	5°C	
T2	Low optimum temperature for dark respiration	<i>M. spicatum</i>	20°C	20°C	
T2	Low optimum temperature for dark respiration	<i>H. verticillata</i>	25°C	25°C	

(Continued)

Table B1 (Continued)

Parameter	Description	Species	Value	Converted Value	Reference
K1	Temperature multiplier for respiration	<i>M. spicatum</i>	0.01	0.01	Calibrated
K1		<i>H. verticillata</i>	0.01	0.01	
K2		<i>M. spicatum</i>	0.98	0.98	
K2		<i>H. verticillata</i>	0.98	0.98	
HTW	Average height-to-weight ratio	<i>M. spicatum</i>	1.27 m g ⁻¹	1.27 m g ⁻¹	Boylen, unpublished data
HTW	Average height-to-weight ratio	<i>H. verticillata</i>	0.416 m g ⁻¹	0.416 m g ⁻¹	Miller (1981)
O2FAC	Oxygen equivalent for macrophyte photosynthesis	<i>M. spicatum</i>	1.0	1.0	Brylinsky and Mann (1973)
O2RESP	Oxygen equivalent for macrophyte dark respiration	<i>M. spicatum</i>	1.2	1.2	Strickland (1960)
PLXGO(1)	Fraction of excreted matter released as PO ₄ -P	<i>M. spicatum</i>	1 - 4%	0.01 - 0.04	Barko and Smart (1980)
PLXGO(1)	Fraction of excreted matter released as PO ₄ -P	<i>H. verticillata</i>	7 - 29%	0.07 - 0.29	Barko and Smart (1980)

(Continued)

Table B1 (Concluded)

Parameter	Description	Species	Value	Converted Value	Reference
PLXGO(2)	Fraction of excreted matter released as $\text{NH}_4\text{-N}$		11%	0.11	Wetzel and Manny (1975)
PLXGO(3)	Fraction of excreted matter released as dissolved organic matter (DOM)		1 - 10%	0.01 - 0.10	Wetzel and Manny (1975)
PLDIGO(1)	Fraction of dead macrophyte that goes to DOM		1 - 10%	0.01 - 0.10	Wetzel and Manny (1975)
PLDIGO(2)	Fraction of dead macrophyte that goes to detritus		29%	0.29	Godshalk and Wetzel (1978)
PLDIGO(3)	Fraction of dead macrophyte that goes to sediment		18%	0.18	Carpenter (1976)

DATE
FILMED
-8